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Two new species of the millipede genus *Epanerchodus* Attems, 1901 from Wuling Mountains, Hunan Province, China (Diplopoda, Polydesmida, Polydesmidae)

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https://zoobank.org/B0C36110-4A06-4092-9429-3E98035995F9

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Abstract

Through morphological comparison and phylogenetic analyses based on the COI gene, two new species of the large Asian millipede genus *Epanerchodus* were identified from cave samples collected in the Wuling Mountains, Hunan Province, China. These species are designated as *Epanerchodus xiaoxiensis* **sp. nov.** and *Epanerchodus shibadongensis* **sp. nov.** This study also provides an updated species checklist for the genus *Epanerchodus* in China, along with a dichotomous key to the cave-dwelling species of the genus in the country.

Key Words

Cave, key, molecular analyses, morphology, taxonomy

Introduction

The East Palaearctic millipede genus *Epanerchodus* Attems, 1901, is one of the largest in the basically Holarctic family Polydesmidae, also being the most species-rich in Asia (Enghoff et al. 2015). To date, 126 species have been described globally (Shinohara 1958; Murakami 1966; Liu and Golovatch 2018; Liu and Huo 2020; Golovatch 2021, 2022; Chen et al. 2023), with the distribution ranging from Central Asia in the northwest, through the Russian Far East, Korea, and Japan in the east, to the Himalayas and China in the south and southeast (Golovatch 2022). In China, 34 species are currently known, predominantly distributed in the provinces of Yunnan, Guizhou, and Sichuan (Zhang and Chen 1983; Chen and Zhang 1990; Zhang and Wang 1992; Geoffroy and Golovatch 2004; Golovatch et al. 2006, 2011, 2012; Golovatch 2013, 2014, 2015, 2021; Golovatch and Geoffroy 2014; Liu and Golovatch 2018; Liu and Huo 2020; Chen et al. 2023). Among these species, 18 are found exclusively outside caves, 15 inhabit karstic caves exclusively, and *E. orientalis* Attems, 1901, has been recorded both inside and outside cave environments (Table 1).

The Wuling Mountains are located at the eastern edge of the Yunnan–Guizhou Plateau in southern China. Spanning four provinces and municipalities—Hunan, Hubei, Guizhou, and Chongqing—they cover an area of approximately 100,000 km^2. Additionally, the Wuling Mountains lie at the intersection of three zoogeographical regions: Central China, South China, and Southwest China. Long recognized as one of the 10 biodiversity hotspots in China (Tang et al. 2006), a significant portion of this region is represented by protected areas. In recent years, we collected millipede specimens during surveys of cave biological resources in the hinterland of the Wuling Mountains, specifically in Xiangxi Tujia and Miao Autonomous Prefecture and

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Table 1. A checklist of the *Epanerchodus* species from China and their distribution.

No.	Species	Locality	References
1	*E. belousovi* Golovatch, 2013	Kangding City, Sichuan Province (outside the cave)	Golovatch 2013
2	*E. bishou* Liu et Huo, 2020	Tianmu Mountain Nature Reserve, Zhejiang Province (outside the cave)	Liu and Huo 2020
3	*E. bispinosus* Golovatch, Mikhaljova et Chang, 2011	Nantou County, Taiwan Province (outside the cave)	Golovatch et al. 2011
4	*E. campus* Liu et Huo, 2020	Yangzhou University, Jiangsu Province (outside the cave)	Liu and Huo 2020
5	*E. chutou* Liu et Golovatch, 2018	Shiqian County, Guizhou Province (inside the cave)	Liu and Golovatch 2018
6	*E. coniger* Liu et Golovatch, 2018	Zhijin County, Guizhou Province (inside the cave)	Liu and Golovatch 2018
7	*E. curtigonopus* Golovatch, Mikhaljova et Chang, 2011	Nantou County, Taiwan Province (outside the cave)	Golovatch et al. 2011
8	*E. draco* Geoffroy et Golovatch, 2004	Zhenxiong County, Yunan Province (inside the cave); Shuicheng County, Guizhou province (inside the cave)	Geoffroy and Golovatch 2004 Liu and Golovatch 2018
9	*E. eurycornutus* Zhang et Wang, 1992	Tianmu Mountain, Zhejiang Province (outside the cave)	Zhang and Wang 1992
10	*E. flagellifer* Golovatch, Mikhaljova et Chang, 2011	Nantou County, Taiwan Provincec (outside the cave)	Golovatch et al. 2011
11	*E. frater* Geoffroy et Golovatch, 2004	Zhenxiong County, Yunan Province (inside the cave)	Geoffroy and Golovatch 2004
12	*E. fuscus* Golovatch, 2015	Lanping County, Yunan Province (inside the cave)	Golovatch 2015
13	*E. gladiatus* Liu et Golovatch, 2018	Wuchuan County, Guizhou Province (inside the cave)	Liu and Golovatch 2018
14	*E. jaegeri* Golovatch, 2014	Taibai Mountain, Shaanxi Province (outside the cave)	Golovatch 2014
15	*E. jiangxiensis* Liu et Golovatch, 2018	Lianhua County, Jiangxi Province (inside the cave)	Liu and Golovatch 2018
16	*E. koreanus* Verhoeff, 1937	Changbai Mountain, Jilin Province (outside the cave)	Golovatch 2014
17	*E. latus* Liu et Golovatch, 2018	Wushan County, Chongqing Municipality (inside the cave)	Liu and Golovatch 2018
18	*E. lipsae* Golovatch et Geoffroy, 2014	Jiangyou City and Beichuan County, Sichuan Province (inside the cave)	Golovatch and Geoffroy 2014; Liu and Golovatch 2018
19	*E. liuae* Golovatch, 2021	Lan Ping County, Yunnan Province (outside the cave)	Golovatch 2021
20	*E. martensi* Golovatch, 2014	Taibai Mountain, Shaanxi Province (outside the cave)	Golovatch 2014
21	*E. orientalis* Attems, 1901	Taichung County, Ilan County, Taitung County, Hualien County, Pingtung County and Kaohsiung County, Taiwan Province (outside the cave);	Golovatch et al. 2011;
		Fenchuan County, Guanxi Province (inside the cave)	Golovatch et al. 2012
22	*E. parvus* Liu et Golovatch, 2018	Cenggong County, Guizhou Province (inside the cave)	Liu and Golovatch 2018
23	*E. pinguis* Golovatch, Mikhaljova et Chang, 2011	Nantou County, Taiwan Province (outside the cave)	Golovatch et al. 2011
24	*E. potanini* Golovatch, 1991	Deqin County, Yunnan Province (outside the cave);	Golovatch 2013;
		Lianhua Mountain and Zhouqu County, Gansu Province (outside the cave);	Golovatch 2014;
		Mianing County, Muli County, Maoxian County, Jiulong County, Yanyuan County and Wenchuan County, Sichuan Province (outside the cave)	Golovatch 2021
25	*E. schawalleri* Golovatch, 2014	Emei Mountain, Sichuan Province (outside the cave)	Golovatch 2014
26	*E. soror* Geoffroy et Golovatch, 2004	Zhenxiong County, Yunnan Province (inside the cave)	Geoffroy and Golovatch 2004; Liu and Golovatch 2018
27	*E. sphaerisetosus* Zhang et Chen, 1983	Jinhua City, Zhejiang Province (outside the cave)	Zhang and Chen 1983
28	*E. stylotarseus* Chen et Zhang, 1990	Guanling County, Pan County, Ceheng County, Xingren County and Shuicheng County, Guizhou Province (inside the cave)	Chen and Zhang 1990; Golovatch et al. 2006; Golovatch et al. 2012; Liu and Golovatch 2018
29	*E. tujiaphilus* Liu et Golovatch, 2018	Longshan County, Hunan Province (inside the cave)	Liu and Golovatch 2018
30	*E. typicus* Golovatch, 2013	Deqin County, Yunnan Province (outside the cave)	Golovatch 2013
31	*E. varius* Geoffroy et Golovatch, 2004	Banqiao County, Lichuan City, Enshi City and Changyang County, Hubei Province (inside the cave);	Geoffroy and Golovatch 2004;
		Beichuan County and Xinlong County, Sichuan Province (inside the cave);	Golovatch and Geoffroy 2014;
		Fengjie County, Wulong County, Pengshui County and Wuxi County, Chongqing Municipality (inside the cave)	Liu and Golovatch 2018
32	*E. wolongensis* Golovatch, 2021	Wenchuan County, Sichuan Province (outside the cave)	Golovatch 2021
33	*E. wuxi* Chen, Zheng et Jiang, 2023	Yintiaoling National Nature Reserve, Chongqing Municipality (inside the cave)	Chen et al. 2023
34	*E. yunnanensis* Golovatch, 2014	Dali City, Yunnan Province (outside the cave)	Golovatch 2014

Zhangjiajie City, Hunan Province. Among these specimens, two species are distinct from any currently described *Epanerchodus*. Through morphological comparison and phylogenetic analyses based on the COI gene, these species are designated as *Epanerchodus xiaoxiensis* sp. nov. and *Epanerchodus shibadongensis* sp. nov. This study also provides an updated species checklist for the genus *Epanerchodus* in China, along with a dichotomous key to the cave-dwelling species of the genus in the country.

Materials and methods

Sampling

The millipede specimens used for morphological examination and molecular analyses were manually collected from caves in Xiangxi Tujia and Miao Autonomous Prefecture and Zhangjiajie City, Hunan Province, from April 2023 to January 2025 (Fig. 1). The specimens were preserved in 75% or 100% ethanol for morphological studies

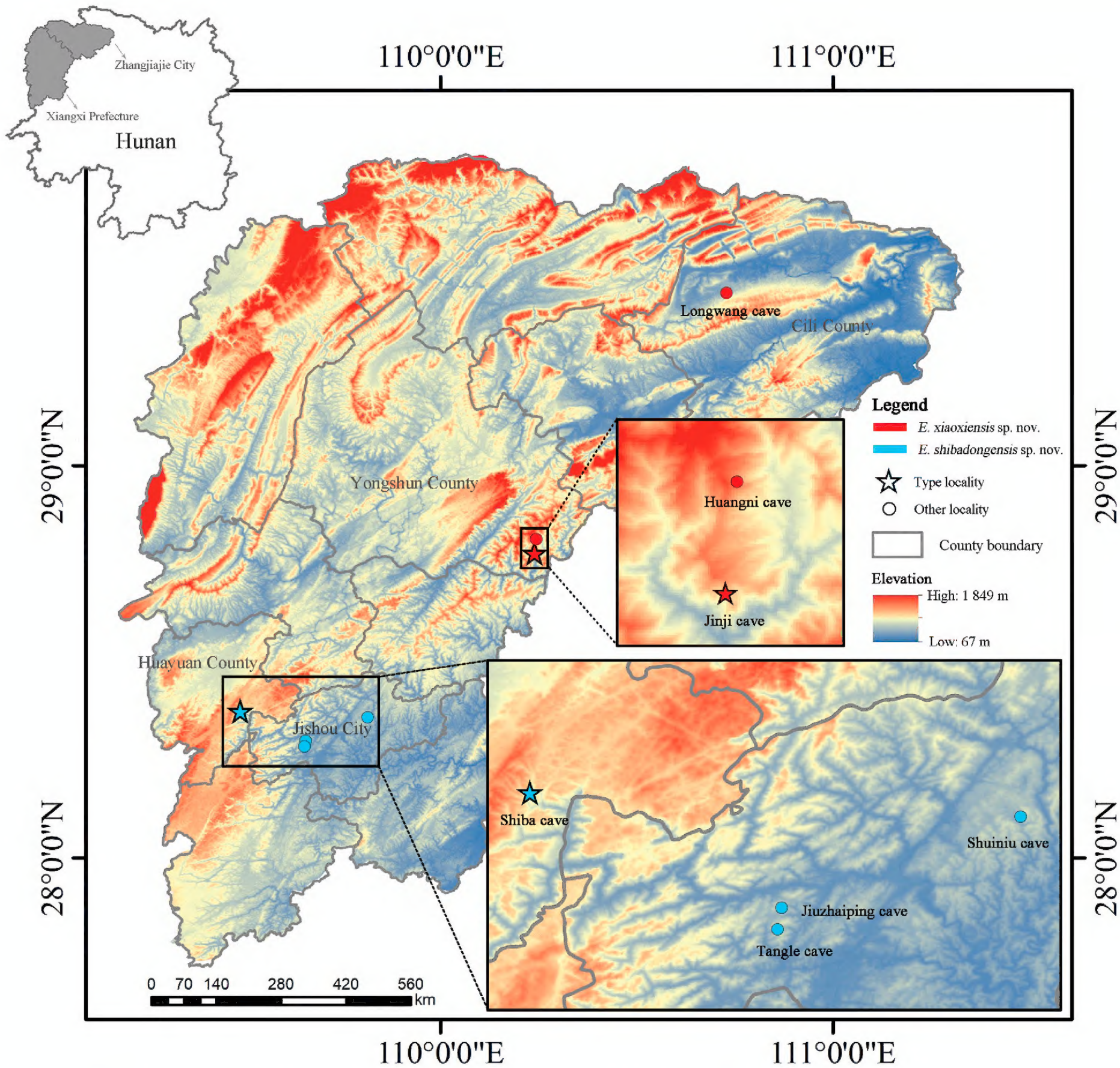

Figure 1. The known distributions of *E. xiaoxiensis* sp. nov. and *E. shibadongensis* sp. nov.

or molecular analyses, respectively. All specimens are deposited in the Animal Museum of the College of Biology and Environmental Sciences, Jishou University (JSU).

The distribution map was generated in ArcGIS v.10.8, using data obtained from the Geospatial Data Cloud.

Morphological examination

Habitat photographs of living specimens were taken with an IQOO Z6 mobile phone. The morphological characters of the specimens were observed and photographed using a Leica M205C stereo microscope equipped with a Leica DMC5400 camera and LAS X 3.7.2 software. Selected characters were further examined and captured using a Zeiss Sigma HD scanning electron microscope at the School of Chemistry and Materials Engineering, Huaihua College. Before SEM observation, pretreatment of specimens involved removal of the tissue to be observed using forceps and a scalpel. Dehydration used a series of ethanol and acetone solutions (95% and 100% ethanol, twice, and ethanol/acetone mixtures of 2:1, 1:1, 1:2, and 0:1), followed by critical point drying, sputter-coating with gold, and examination using a Zeiss Field Emission Scanning Electron Microscope (Sigma HD) at magnifications ranging from 100x to 15,000x. Images were processed and edited using Adobe Photoshop CS6.

The terminology employed in this study follows that of Golovatch (2014), Enghoff et al. (2015), and Liu and Golovatch (2018).

COI gene sequencing and phylogenetic analysis

Total DNA extraction was performed using Qiagen DNeasy Blood and Tissue Kits, according to the manufacturer's instructions. Fragments of the mitochondrial COI

Table 2. Sequences information, locality, voucher, and COI GenBank accession numbers used in this study for molecular analyses.

No.	Species	Locality	Voucher	GenBank
1	*Epanerchodus shibadongensis* Li, Deng &Liu, sp. nov.	Jishou, Hunan, China	JSUEpanerchodus01	PQ901443
2	*Epanerchodus shibadongensis* Li, Deng & Liu, sp. nov.	Jishou, Hunan, China	JSUEpanerchodus02	PQ901444
3	*Epanerchodus xiaoxiensis* Li, Deng & Liu, sp. nov.	Yongshun, Hunan, China	JSUXiaoxi03	PV665423
4	*Epanerchodus xiaoxiensis* Li, Deng & Liu, sp. nov.	Yongshun, Hunan, China	JSUXiaoxi04	PV665424
5	*Epanerchodus polymorphus* Mikhaljova & Golovatch, 1981	Vladivostok, Primorsky Krai, Russia	MPE04779	MN232239
6	*Epanerchodus polymorphus* Mikhaljova & Golovatch, 1981	Vladivostok, Primorsky Krai, Russia	MPE04778	MN232240
7	*Epanerchodus kunashiricus* Mikhaljova, 1988	Yuzhno-Kurilsky, Sakhalin Oblast, Russia	MPE03455	MN232234
8	*Epanerchodus koreanus* Verhoeff, 1937	Russia	MPE04764	MN232238
9	*Epanerchodus lacteus* Shinohara, 1958	Tsukuba, Ibaraki, Japan	MPE04884	MT740082
10	*Schizoturanius tabescens* Stuxberg, 1876	Ust-Kansky, Altai Republic, Russia	MPE04781	MN232242

gene were amplified via PCR using universal primer pairs HCO2198-JJ and LCO1490-JJ designed for invertebrates (Zhao et al. 2021). The successfully amplified PCR products were purified and sequenced by Hunan Qingke Biotechnology Co., Ltd. (China). The COI sequences were validated using BLAST and subsequently registered in GenBank with corresponding accession numbers.

For molecular analyses, a dataset of 10 COI sequences was compiled, including six sequences retrieved from GenBank (Table 2). Among these sequences, nine belong to *Epanerchodus*. The sequence of *Schizoturanius tabescens* was used as the outgroup. All sequences were aligned using MAFFT and manually checked for accuracy. In PhyloSuite v.1.2.3 (Zhang et al. 2020), based on the COI sequences, we constructed both Bayesian phylogenies using MRBAYES v.3.2.7a (Ronquist et al. 2012) and maximum likelihood phylogenies using IQ-TREE v.2.2.0 (Nguyen et al. 2015). Maximum likelihood phylogenies were inferred under the GTR+I+G4+F model selected by MODELFINDER v.2.2.0 (Kalyaanamoorthy et al. 2017) according to the AIC criterion for 50,000 ultrafast bootstraps (Minh et al. 2013). Bayesian inference phylogenies were inferred under the GTR+G+F model (2 parallel runs, 2×10^6 generations) selected by MODELFINDER v.2.2.0 (Kalyaanamoorthy et al. 2017) according to the BIC criterion, with the initial 25% of sampled data discarded as burn-in. Additionally, uncorrected p-distances of COI sequences were calculated in MEGA v.11.0.13 (Tamura et al. 2021).

Figure 2. Live specimens of *E. xiaoxiensis* sp. nov.

Results

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Polydesmida Pocock, 1887
Family Polydesmidae Leach, 1815
Genus *Epanerchodus* Attems, 1901

***Epanerchodus xiaoxiensis* Li, Deng & Liu, sp. nov.**
https://zoobank.org/793D1741-5FB4-4B14-8F6E-7D2380B5EE8D
Figs 2–5

Material examined. ***Holotype.*** China: • ♂ (JSUXiaoxi03); Hunan Province, Xiangxi Tujia and Miao Autonomous Prefecture, Yongshun County, Xiaoxi National Nature Reserve, Jinji Cave; 28°46'48"N, 110°13'48"E, ca. 890 m a.s.l.; 12 August 2024, S. Li, H.J. Deng, Z.X. Liu, and Y. Tang leg. ***Paratypes.*** China: • 3 ♂♂, 3 ♀♀ (JSUXiaoxi04-JSUXiaoxi09); same data as holotype. China: • 2 ♂♂, 4 ♀♀ (JSUXiaoxi10-JSUXiaoxi15); same data as holotype; Hunan Province, Xiangxi Tujia and Miao Autonomous Prefecture, Yongshun County, Xiaoxi National Nature Reserve, Huangni Cave; 28°48'57"N, 110°14'19"E, ca. 31043 m a.s.l.; 4 May 2023, H.J. Deng, Q.J. Wu, D.Q. Xiang, and Z.X. Liu leg. China: • 5 ♂♂, 3 ♀♀ (JSUXiaoxi16-JSUXiaoxi23); same data as holotype; Hunan Province, Zhangjiajie City, Cili County, Longwang Cave; 29°26'27"N, 110°43'41"E, ca. 380 m a.s.l.; 21 September 2024, S. Li, Y.Z. Zou, Z.X. Liu, and Y. Tang leg.

Etymology. The specific name derives from the type locality, Xiaoxi National Nature Reserve. Adjective.

Diagnosis. Adult males of *E. xiaoxiensis* sp. nov. are distinct from other *Epanerchodus* species based on the following combination of characters: (1) body smaller in size, length of body ca 11–13 mm (males), width of body ca 1.5–1.6 mm (males); (2) gonopodal prefemorite

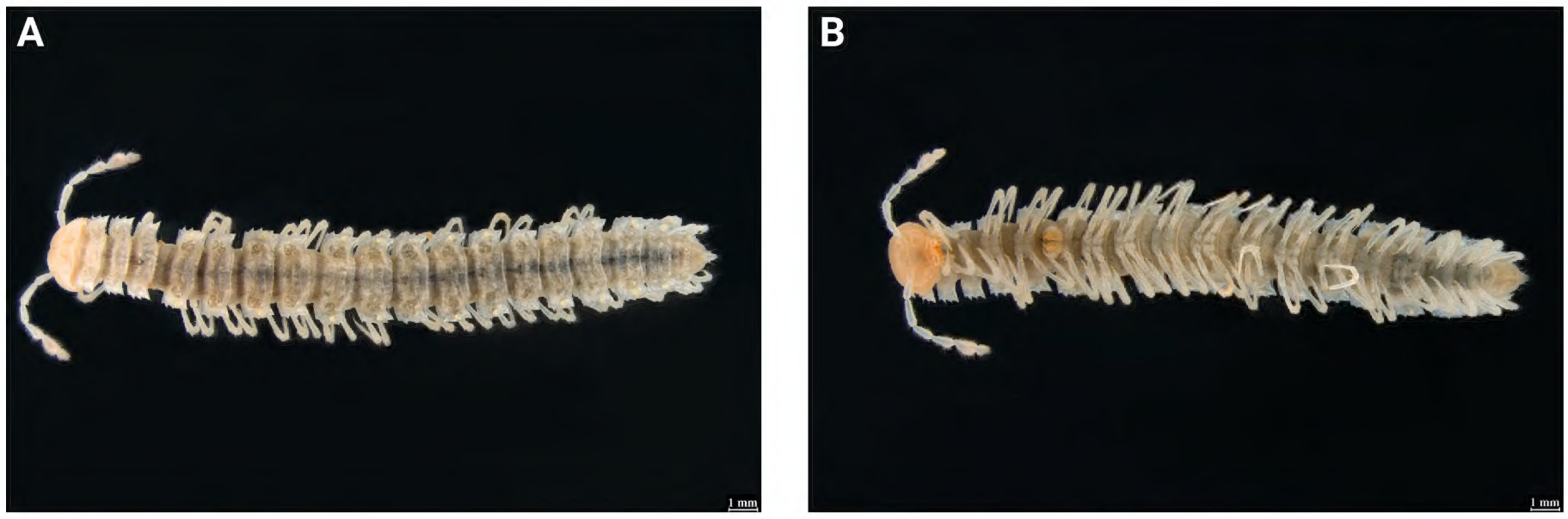

Figure 3. *E. xiaoxiensis* sp. nov., male paratype from Jinji Cave. **A.** Habitus, dorsal view; **B.** Habitus, ventral view.

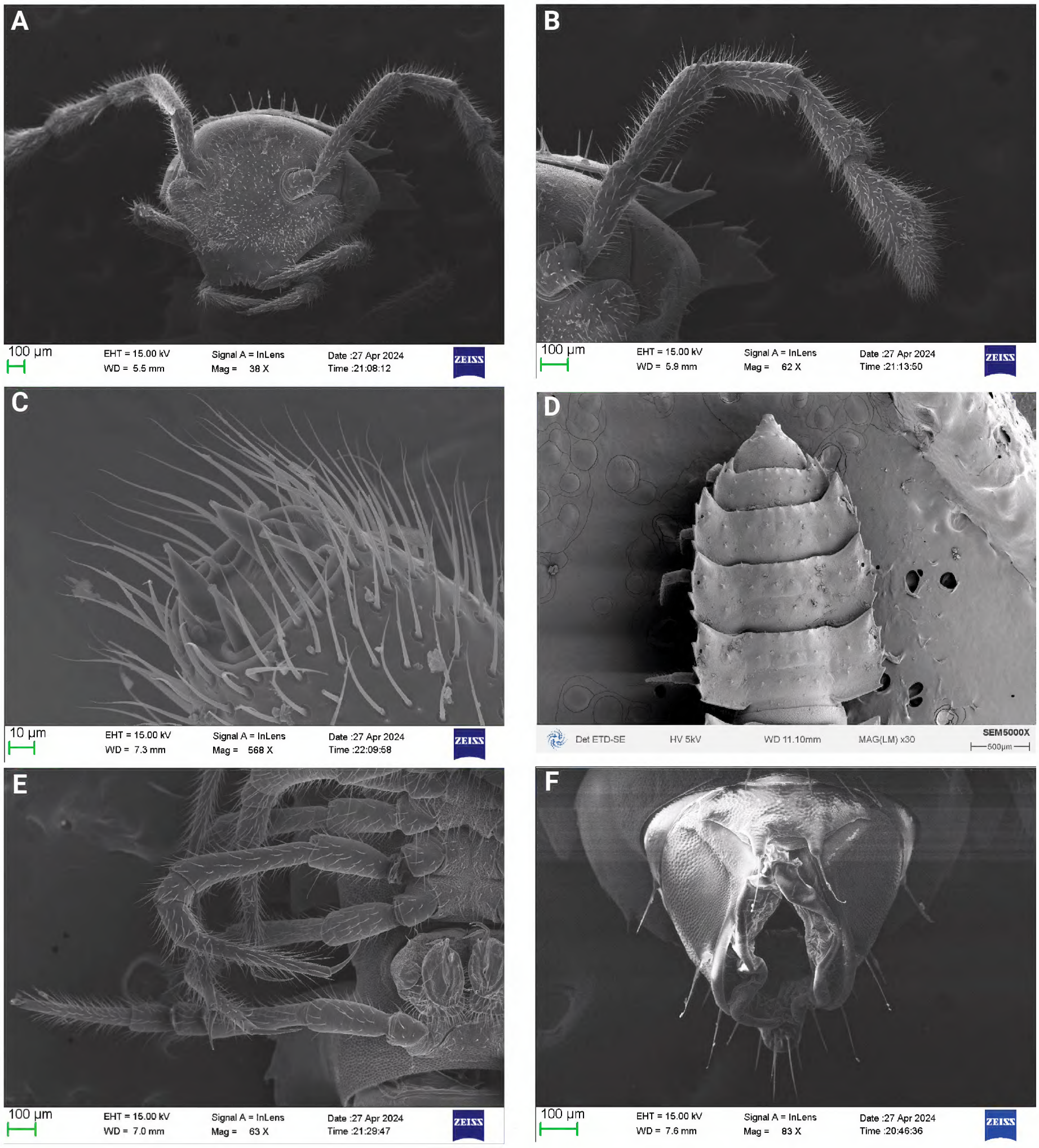

Figure 4. *E. xiaoxiensis* sp. nov., male paratype from Jinji Cave. **A.** Head, ventral view; **B.** Left antenna; **C.** Antennomere 7; **D.** Posterior part of body, dorsal view; **E.** Legs; **F.** Telson, ventral view.

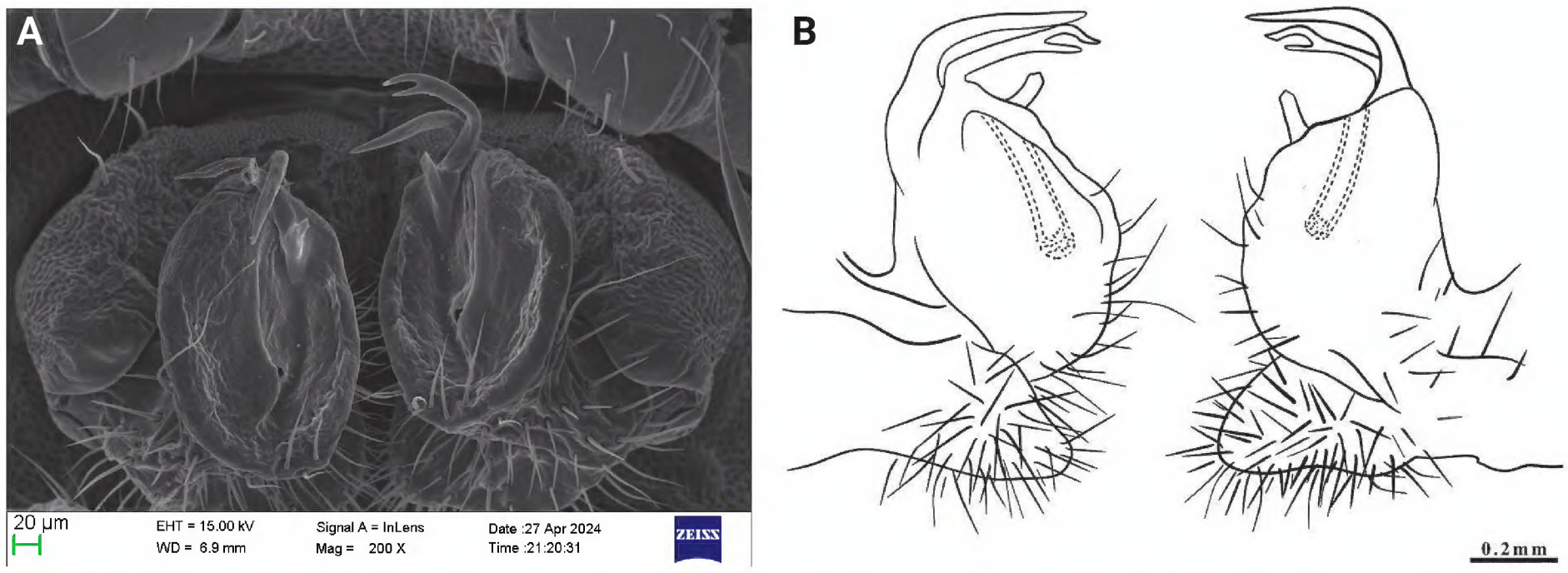

Figure 5. *E. xiaoxiensis* sp. nov., male paratype from Jinji Cave. **A.** Gonopods *in situ*, ventral view; **B.** Left gonopod, mesal and sublateral views, respectively. Abbreviations: cl = clivus; en = endomere; ex = exomere; p = process; sg = seminal groove.

stout and short, about 1/3 as long as telopodite (Fig. 5B); (3) gonopod endomere with a bifurcated shape at the end (Fig. 5B); (4) gonopod exomere long and pointed, sword-shaped, as long as gonopod endomere (Fig. 5B).

Diagnostic remarks. Based both on the geographic distribution and morphological characters, the new species seems to be especially close to *E. tujiaphilus* (Liu and Golovatch 2018), from Longshan County, Hunan Province, in which the endomere tip is bifid and the exomere spiniform. However, the two species compared are clearly different: (1) body smaller and transparent white (Fig. 2), *vs.* body larger and yellowish in *E. tujiaphilus*; (2) the gonopod endomere is as long as the gonopod exomere (Fig. 5A), *vs.* the gonopod endomere is considerably longer than the gonopod exomere.

Description. Based on type specimens. Length of body *ca* 11–13 mm (males) or 12–15 mm (females). Width of body *ca* 1.5–1.6 mm (males) or 1.7–1.8 mm (females). ***Coloration*:** Live specimens semi-transparent to whitish (Fig. 2); in alcohol, light yellowish (Fig. 3). ***Body*:** Adults with 20 segments. In width, head < collum < segment 2 < 3 < 4 < 5 < 6 < 7–16, thereafter body gradually tapering posteriorly towards telson. ***Head*:** vertex pubescent, epicranial suture conspicuous (Fig. 4A), frons with dense short pubescence (Fig. 4A). Labrum relatively flat and long, with a row of three sharp teeth (Fig. 4A). Antennae long and slender, slightly clavate, densely setose, *in situ* extending past ring 4 when extended posteriorly (Fig. 3B); in length, antennomere 7 < 1 < 4 = 5 < 2 = 6 < 3 (Fig. 4B); antennomeres 5 and 6 each with a distodorsal group of sensilla basiconica (Fig. 4B); antennomere 6 thick and swollen; antennomere 7 with four sensory cones apically (Fig. 4C). ***Exoskeleton*:** Collum semi-oval, sparsely setose, with a lateral incision on each side (Figs 3A, 4B). Paraterga well-developed and mostly slightly upturned dorsally (Fig. 4D), midbody metaterga *ca* 1.6 times as wide as prozona (Fig. 3A). Anterior margins of metaterga forming shoulders (Fig. 3A). Caudolateral corners of paraterga starting with ring 2 clearly projecting posteriorly past tergal margin and strongly acuminate (Fig. 3A). Integument shining, translucent, prozona very delicately alveolate (Fig. 3A). Constriction between pro- and metazona narrow and smooth (Fig. 3B). Metatergal sculpture faint, with three irregular transverse rows of setigerous polygonal bosses (Fig. 4D). Sulcus between front and middle rows of setae distinct; that between middle and caudal rows obscure (Fig. 4D). Tergal setae visible, short. Poreless and pore-bearing paraterga with 3 or 4 faint incisions at lateral margin, respectively. Ozopores located between last and penultimate marginal incisions (Fig. 4D). Pore formula normal: 5, 7, 9, 10, 12, 13, 15–19. Epiproct process short, conical, slightly surpassing paraprocts caudally, pre-apical lateral papillae small, with two long setae (Fig. 4F). Hypoproct trapezoid, with two setigerous, conical papillae at caudal margin (Fig. 4F). Sterna sparely setose, cross-impressions shallow (Fig. 3B). Rings 5–19 each with two pairs of long legs, tarsi longest, claws curved ventrad and pointed, legs *ca* 1.5 times as long as body height in both sexes. Neither sphaerotrichomes nor sternal cones, prefemora not bulged laterally (Fig. 4E). ***Gonopods*:** coxite short and stout; prefemorite densely setose, as usual, about 1/3 as long as telopodite; femorite with a finger-shaped process (p); clivus (cl) short; endomere (en) with a bifurcated shape at the end; exomere (ex) long and pointed, sword-shaped, as long as endomere; seminal groove (sg) running mostly mesally, then ultimately entering an accessory seminal chamber (Fig. 5).

Epanerchodus shibadongensis Li, Deng & Liu, sp. nov.

https://zoobank.org/9245E44F-E074-48A5-B4E0-DA10A8461247

Figs 6–9

Material examined. ***Holotype.*** China: • ♂ (JSU*Epanerchodus*03); Hunan Province, Xiangxi Tujia and Miao Autonomous Prefecture, Huayuan County, Shibadong Village, Shiba Cave; 28°22'49"N, 109°49'30"E, ca.

Figure 6. Live specimens of *E. shibadongensis* sp. nov.

620 m a.s.l., 17 November 2024, S. Li, Z.X. Liu, and Y.Z. Zou leg. ***Paratypes.*** China: • ♂, 3 ♀♀ (JSU*Epanerchodus*04-JSU*Epanerchodus*07); same data as holotype; Hunan Province, Xiangxi Tujia and Miao Autonomous Prefecture, Jishou City, Tangle Cave; 28°18'9"N, 109°39'2"E, ca. 340 m a.s.l.; 8 May 2023, H.J. Deng, H.Y. Xiang, and Z.X. Liu leg. China: • 2 ♂♂, 6 ♀♀ (JSU*Epanerchodus*08-JSU*Epanerchodus*15); same data as holotype; Hunan Province, Xiangxi Tujia and Miao Autonomous Prefecture, Jishou City, Jiuzhaiping Cave; 28°29'19"N, 110°6'28"E, ca. 340 m a.s.l.; 22 September 2023, S. Li, Y.Z. Zou, Z.X. Liu leg.

Etymology. The specific name is derived from the type locality, Shibadong Village and Shiba Cave. Adjective.

Diagnosis. Adult males of *E. shibadongensis* sp. nov. are distinct from other species of *Epanerchodus* based on the following combination of characters: (1) body larger in size, length of body *ca* 21–23 mm (males), width of body *ca* 3.1–3.3 mm (males); (2) a simple gonopod structure (Fig. 9B); (3) a short vertical spiniform process present in a mid-lateral position of the endomere (Fig. 9C).

Diagnostic remarks. This new species is similar to *Epanerchodus chutou* Liu and Golovatch 2018, from Shiqian County, Guizhou Province (Liu and Golovatch 2018), in which the gonopod endomere shows a spiniform process and a missing gonopod exomere. However, the two species compared differ as follows: (1) gonopodal prefemorite about 1/3 as long as telopodite, *vs.* prefemorite about 2/3 as long as telopodite in *E. chutou*; (2) gonopod endomere with a vertical spiniform process near the middle, *vs.* gonopod endomere with a slender, spiniform, basal process in *E. chutou*; (3) gonopod endomere lamellar, crescent-shaped apically, *vs.* gonopod endomere hoe-shaped, folded at the edge, flush apically in *E. chutou*; (4) clivus long and high, *vs.* clivus short in *E. chutou*.

Description. Based on type specimens. Length of body *ca* 21–23 mm (males) or 22–24 mm (females). Width of body *ca* 3.1–3.3 mm (males) or 3.3–3.6 mm (females). ***Coloration*:** Live specimens whitish (Fig. 6); in alcohol pale yellowish green (Fig. 7). ***Body*:** Adults with 20 segments. In width, head < collum < segments 2–3 < 3–6 < 7–9 < 11–13, thereafter body gradually tapering posteriorly towards telson. ***Head*:** vertex covered with short sparse setae, epicranial suture conspicuous, frons densely clothed with short pubescence (Fig. 8A). Labrum with a row of three sharp teeth, mandibular stipes inflated (Fig. 8B). Antennae long and slender, slightly clavate, densely covered with short setae, in length, antennomere 1 < 7 < 4 < 5 = 2 = 6 < 3, antennomere 6 inflated, antennomere 7 with four sensory cones apically (Fig. 8A). ***Exoskeleton*:** Collum subelliptical, with a row of setae along anterior margin, two faint lateral incisions on each side. Paraterga obvious, midbody metaterga *ca* 2.0 times as wide as prozona (Fig. 7B). Paraterga on collum and rings 2–13 clearly upturned dorsally above a faintly convex dorsum, other paraterga flat (Fig. 7A). Caudolateral corners of paraterga strongly acute, collum, rings 2–5, and rings 13–19 projecting posteriorly past rear tergal margin (Fig. 7A). Constriction between pro- and metazona narrow and smooth (Fig. 7B). Metatergal sculpture faint, with three irregular transverse rows of setigerous polygonal bosses. Sulcus between middle and caudal rows of setae deeper than that between front and middle rows. Tergal setae mostly visible, short. Poreless and pore-bearing paraterga with 3 or 4 faint incisions at lateral margin, respectively. Ozopores located between last and penultimate marginal incisions. Pore formula normal: 5, 7, 9, 10, 12, 13, 15–19. Epiproct process short, conical, slightly surpassing paraprocts caudally, pre-apical lateral papillae small, with two long setae (Fig. 7D). Hypoproct trapezoid, with two triangular and conical papillae at caudal margin.

Figure 7. *E. shibadongensis* sp. nov., male paratype from Shiba Cave. **A.** Habitus, dorsal view; **B.** Habitus, ventral view.

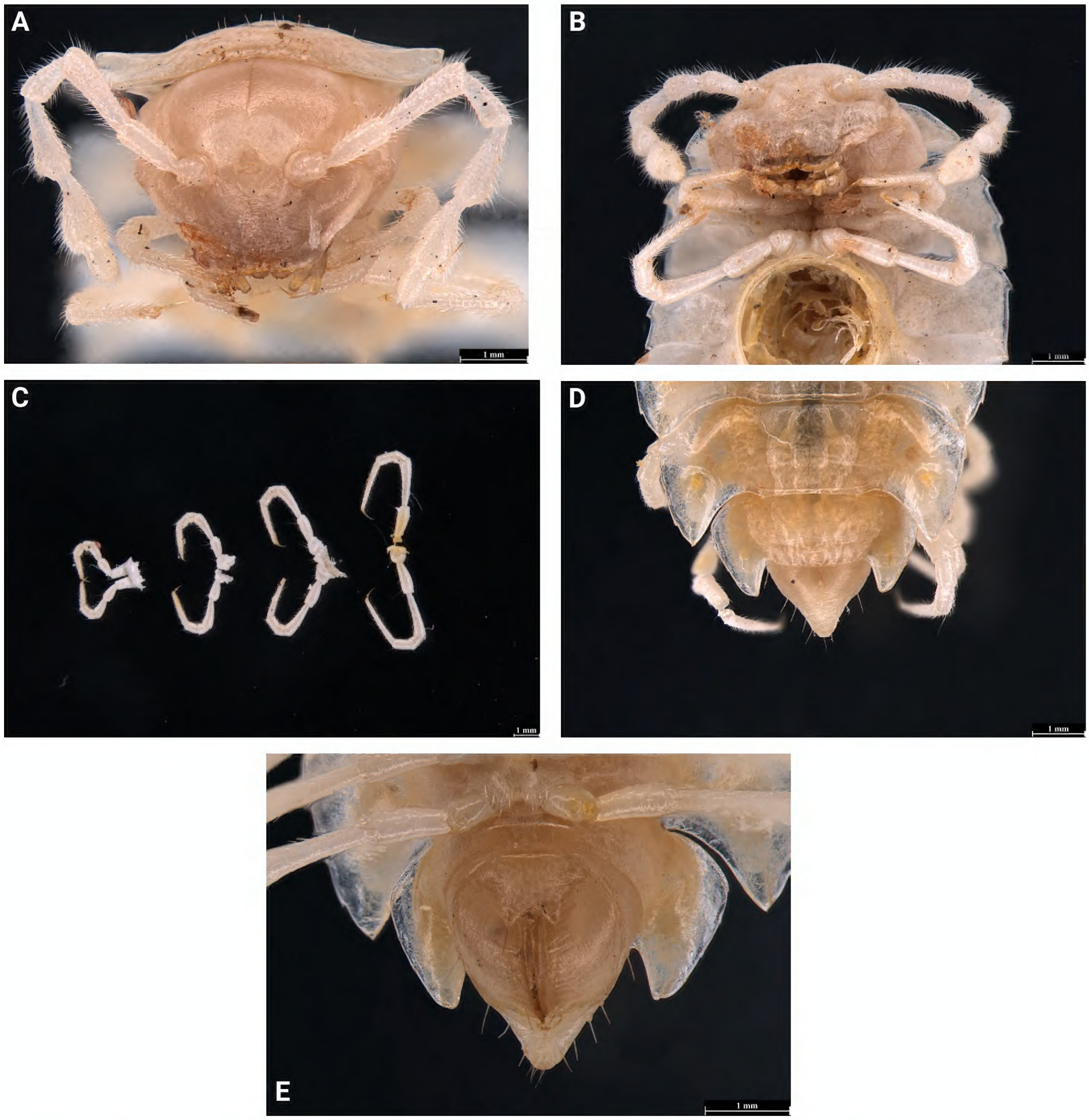

Figure 8. *E. shibadongensis* sp. nov., male paratype from Shiba Cave. **A.** Head, ventral view; **B.** Head, frontal view; **C.** Legs 1, 2, 3, and 20, posterior view; **D.** Posterior part of body, dorsal view; **E.** Telson, ventral view.

Sterna sparely setose, cross-impressions shallow (Fig. 7E). Legs 1 shorter, coxa longer, following legs slender, densely setose, claw sharp, spiniform, curved mesad, lacking sphaerotrichomes, prefemora not bulged laterally, about 2 times as long as body height in both sexes (Fig. 8C). ***Gonopods*:** (Fig. 9) coxite robust; prefemorite clothed with dense long setae, as usual, about 1/3 as long as telopodite; telopodite inflated; clivus (cl) long and high; endomere (en) lamellar, crescent-shaped apically, with a vertical spiniform process (a) at 2/3; exomere absent; a short, digitiform, lateral process (p) about 1/4 the length of endomere and near endomere base; seminal groove (sg) starting from lateral side of lateral process, debauching medially from femorite into an accessory seminal chamber.

Molecular analyses

The dataset used for phylogenetic analyses comprised a total of 10 COI sequences, each 646 bp in length. The results are presented in Fig. 10, and the p-distance values are provided in Table 3. The phylogenetic analysis reveals that *E. shibadongensis* sp. nov. and *E. xiaoxiensis* sp. nov. form

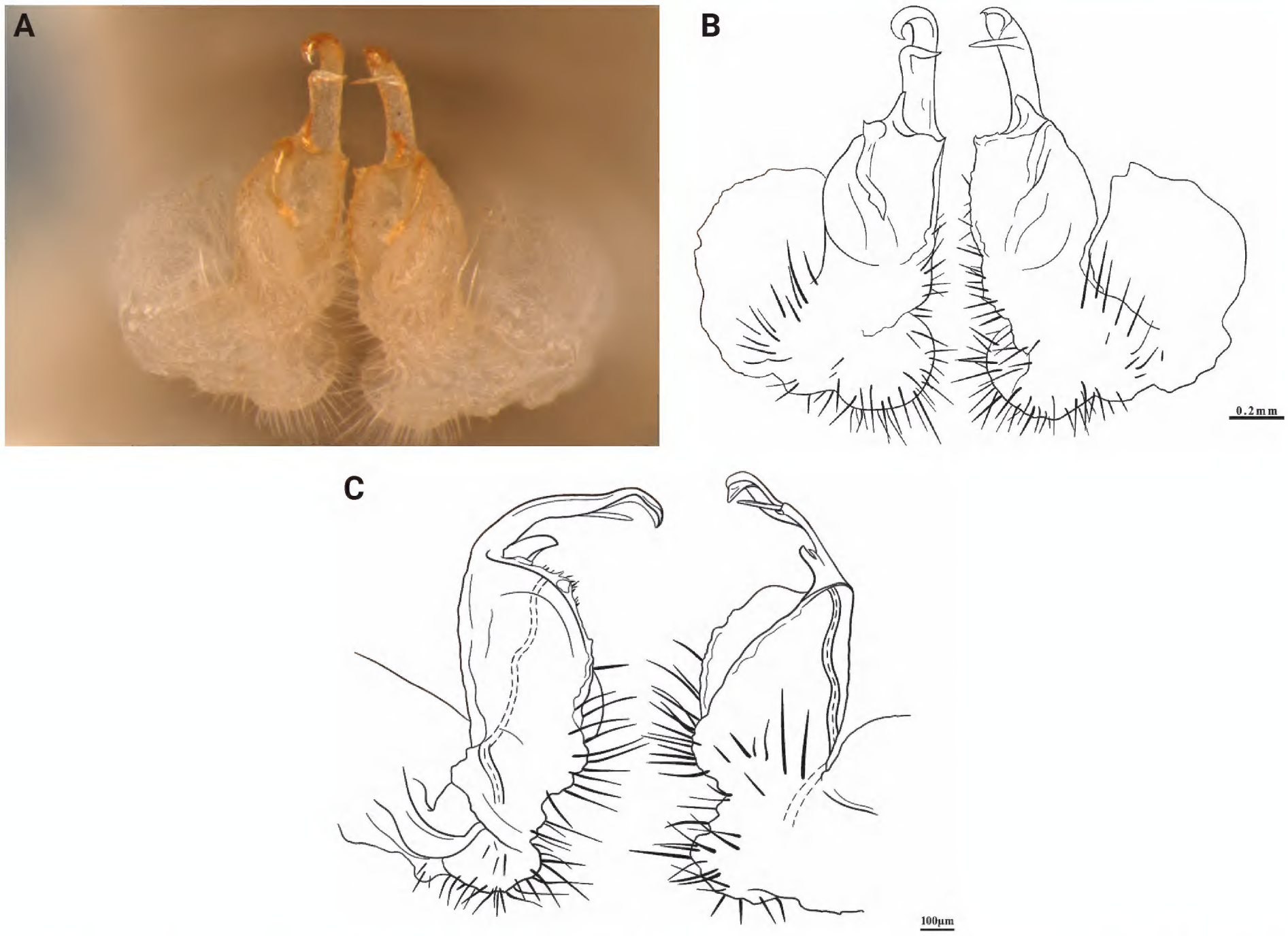

Figure 9. *Epanerchodus shibadongensis* sp. nov., male paratype from Shiba Cave. **A.** Gonopods *in situ*, ventral view; **B.** Gonopods ventral view; **C.** Left gonopod, mesal and lateral views, respectively. Abbreviations: a = spiniform process; cl = clivus; en = endomere; p = process; sg = seminal groove.

Table 3. Uncorrected *p*-distances (%) among *Epanerchodus* species inferred from mitochondrial COI gene fragments (646 bp).

Species	1-2	3-4	5-6	7	8
1-2 *Epanerchodus shibadongensis* sp. nov.	0.000				
3-4 *Epanerchodus xiaoxiensis* sp. nov.	0.137–0.150	0.011			
5-6 *Epanerchodus polymorphus*	0.122–0.124	0.152–0.167	0.018		
7 *Epanerchodus kunashiricus*	0.128	0.158–0.167	0.088	0.000	
8 *Epanerchodus koreanus*	0.124	0.158–0.165	0.118–0.120	0.124	0.000
9 *Epanerchodus lacteus*	0.117	0.153–0.163	0.088–0.098	0.112	0.122

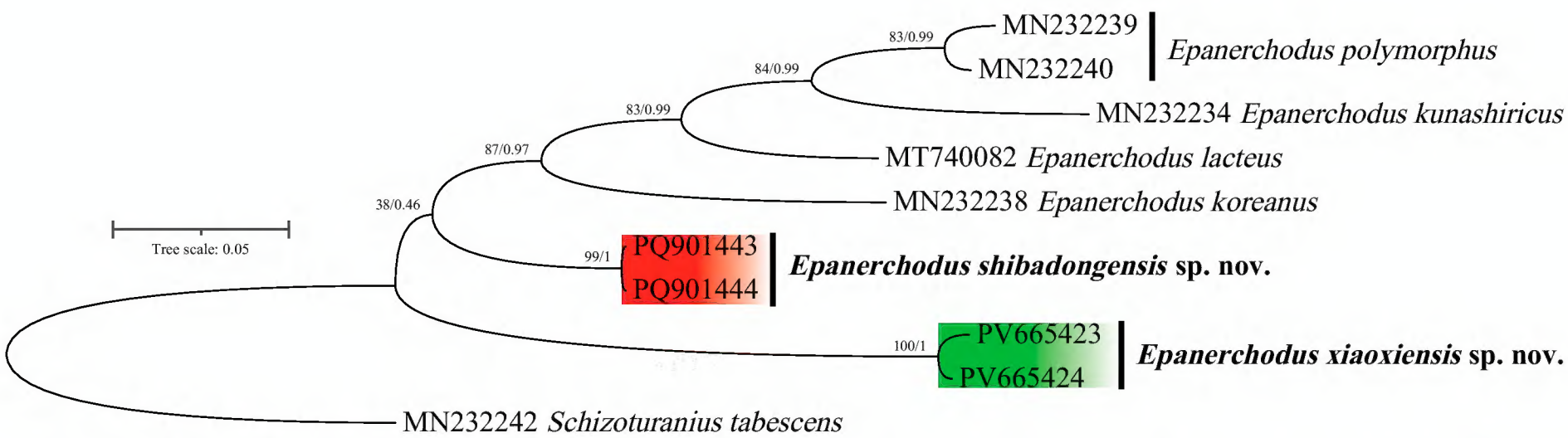

Figure 10. Phylogenetic tree of the genus *Epanerchodus* inferred from COI gene fragments (646 bp) using maximum-likelihood analysis. The numbers above the branches indicate support values from two tests: the SH-like approximate likelihood ratio test and Bayesian posterior probabilities.

distinct and well-supported clades with high bootstrap values (Fig. 10). *E. shibadongensis* sp. nov. exhibits p-distances ranging from 11.7% to 15% when compared to other species, while *E. xiaoxiensis* sp. nov. shows p-distances ranging from 13.7% to 16.7% (Table 3). These findings, together with the observed morphological and genetic differences, indicate that both species are clearly distinct from all known congeners with available COI sequence data.

Key to cave *Epanerchodus* species known from China, chiefly based on males

1 Exomere present 2
– Exomere absent 10
2 Exomere sword-shaped 3
– Exomere not sword-shaped 5
3 Endomere symmetrically bifurcated at end ..... *E. xiaoxiensis* sp. nov.
– Endomere asymmetrically forked at end 4
4 Exomere peg-shaped ..... *E. lipsae*
– Exomere not peg-shaped, but trifurcate ..... *E. fuscus*
5 Endomere with a vertical spiniform process at base ..... *E. shibadongensis* sp. Nov.
– Endomere without vertical spiniform process at base 6
6 Endomere hook-shaped and bifurcate ..... *E. orientalis*
– Endomere not hook-shaped 7
7 Paraterga with 5 to 6 lateral incisions ..... *E. jiangxiensis*
– Paraterga with 3 to 4 lateral incisions 8
8 Endomere with apical denticles at end 9
– Endomere without apical denticles at end 11
9 Endomere with subapical lobes ..... *E. wuxi*
– Endomere beak-shaped and without subapical lobe ..... *E. parvus*
10 Endomere hoe-shaped with a slender spiniform process at base ..... *E. chutou*
– Endomere not hoe-shaped 12
11 Endomere sword-shaped with a circular bulge at base ..... *E. gladiatus*
– Endomere not sword-shaped 13
12 Sterna with sharp cones ..... *E. coniger*
– Sterna without cone 14
13 Legs with sphaerotrichomes ..... *E. frater*
– Legs without sphaerotrichome 15
14 Endomere baciliform with three teeth at end ..... *E. stylotarseus*
– Endomere banded 16
15 Paraterga broad, extending metatergite to *ca* 2.3 × width of prozonite ..... *E. latus*
– Paraterga relatively narrow 17
16 Gonopodal femorite with spines ..... *E. varius*
– Gonopodal femorite without spine ..... *E. tujiaphilus*
17 Antennae especially long, *in situ* extending past ring 5 ..... *E. draco*
– Antennae shorter, *in situ* extending only past ring 4 ..... *E. soror*

Discussion

With the discovery of two new millipede species in Hunan Province, *E. xiaoxiensis* sp. nov. and *E. shibadongensis* sp. nov., the global richness of *Epanerchodus* has now increased to 128 species, of which 36 are recorded in China, including three documented from Hunan Province. Across Hunan, Hubei, and Guizhou provinces and Chongqing Municipality, 13 *Epanerchodus* species are known, accounting for approximately 36% of the Chinese *Epanerchodus* fauna. This highlights the region's rich millipede diversity and underscores the need for further systematic investigations.

During the course of our phylogenetic analyses, it became evident that the molecular data available for the genus *Epanerchodus* in GenBank are highly limited. Although the genus comprises more than 120 species, only 14 COI sequences have been deposited (five of which lack species identification), four of which were newly generated in this study. This paucity of genetic data represents a substantial obstacle to accurate species identification.

Furthermore, some scholars have investigated the potential morphological adaptations of millipedes to cave environments and identified four characteristics of troglobitic millipedes: a longer body, lighter body color, elongated femora, and elongated tarsi of walking legs (Liu et al. 2017). The two newly described species in this study largely conform to these characteristics and have only been found in caves to date. Therefore, we consider them to belong to the

cave-dwelling species of the genus *Epanerchodus*. Given the extreme and highly fragile nature of cave ecosystems, it is of utmost importance to enhance protection efforts.

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